



Attachment 1

IN THE UNITED STATES PATENT AND TRADEMARK OFFICE

In re Patent Application of:

BORONAT *et al.*

Appl. No.: 09/987,025

Filed: November 13, 2001

For: Nucleic Acid Sequences to Proteins  
Involved in Isoprenoid Synthesis

Art Unit: 1638

Examiner: Not Yet Assigned

Atty. Docket: 16515.102

DECLARATION PURSUANT TO 37 C.F.R. § 1.132

Commissioner for Patents  
Washington, DC 20231

Dear Sir:

I, Henry E. Valentin, declare that:

- 1 I have been employed by Monsanto Company since September 1996.
- 2 On 07/18/2002, I received from Narciso Campos, PhD, a plasmid designated "pDXR-AT", which is referenced in the above referenced application at page 28 of the specification in Example 4.
- 3 On 09/16/2002, I received from Narciso Campos, PhD, a plasmid designated "pBAD-DXR", which is referenced at page 30 of the specification in Examples 5 and 6.
- 4 At my request, both pDXR-AT and pBAD-DXR were transformed into *Escherichia coli*, maxipreped, and the sequence of the cDNA insert was determined.
- 5 I hereby certify that the plasmids pBAD-DXR and pDXR-AT were sent by Federal Express on September 26<sup>th</sup> 2002 to the American Type Culture Collection (ATCC, 10801 University Blvd.; Manassas, VA 20110-2209, USA) under the Budapest Treaty, and were received by the ATCC on September 27, 2002, and were accorded ATCC accession numbers PTA-4728 and PTA-4727, respectively. The deposited biological materials, respectively, were derived from aliquots of vials of plasmid pBAD-

DXR and PDXR-At, which had been sent to me by Narciso Campos and were in my continuous custody and control until the date of the deposit.

6 I further declare that all statements made herein of my own knowledge are true and that all statements made on information and belief are believed to be true; and further that these statements are made with the knowledge that willful false statements and the like so made are punishable by fine or imprisonment, or both, under Section 1001 of Title 18 of the United States Code, and that such willful false statements may jeopardize the validity of the above-captioned patent application or any patent which issues therefrom.



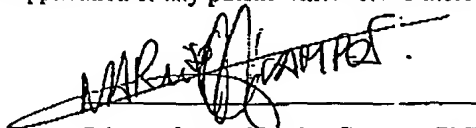
Printed Name: Henry E. Valentin, PhD

Title: Research Manager

Date: 10/08/2002

Boronat *et al.*  
Attorney Docket No: 16516.102  
Page 2

5 I further declare that all statements made herein of my own knowledge are true and that all statements made on information and belief are believed to be true; and further that these statements are made with the knowledge that willful false statements and the like so made are punishable by fine or imprisonment, or both, under Section 1001 of Title 18 of the United States Code, and that such willful false statements may jeopardize the validity of the above-captioned patent application or any patent which issues therefrom.



Printed Name: Narciso Campos, PhD

Title: \_\_\_\_\_

Date: OCTOBER 11, 2002

## Update on Isoprenoid Biosynthesis

# Elucidation of the Methylerythritol Phosphate Pathway for Isoprenoid Biosynthesis in Bacteria and Plastids. A Metabolic Milestone Achieved through Genomics<sup>1</sup>

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Plants synthesize an enormous variety of metabolites that can be classified into two groups based on their function: primary metabolites, which participate in nutrition and essential metabolic processes within the plant, and secondary metabolites (also referred to as natural products), which influence ecological interactions between plants and their environment (Croteau et al., 2000). Isoprenoids (also called terpenoids) are the most functionally and structurally varied group of plant metabolites. Isoprenoids are synthesized in all organisms but are especially abundant and diverse in plants, with tens of thousands of compounds reported to date (Chappell, 1995, 2002; McGarvey and Croteau, 1995; Croteau et al., 2000). Many isoprenoids are present in all plants and act as primary metabolites with roles in respiration, photosynthesis, and regulation of growth and development. However, the highest variety of isoprenoids is secondary metabolites that function in protecting plants against herbivores and pathogens, in attracting pollinators and seed-dispersing animals, and as allelochemicals that influence competition among plant species (Croteau et al., 2000; Chappell, 2002). Many compounds with important commercial value as flavors, pigments, polymers, fibers, glues, waxes, drugs, or agrochemicals are secondary metabolites of isoprenoid origin. Each plant species synthesizes a specific array of isoprenoid secondary metabolites, and most of them (including rubber and the anticancer drug taxol) are produced only in a few wild or semiwild plant species. Although genetic engineering appears to be a powerful tool to direct the production of both primary and secondary isoprenoid products in plants, only a partial knowledge of the pathways involved in the biosynthesis of their precursors was available until very recently.

## ISOPRENOID BIOSYNTHESIS. A TALE OF TWO PATHWAYS

Despite their diversity of functions and structures, all isoprenoids derive from the common five-carbon ( $C_5$ ) building units isopentenyl diphosphate (IPP) and its isomer dimethylallyl diphosphate (DMAPP), also called isoprene units (Fig. 1). The simplest isoprenoids, like isoprene (a volatile product released from photosynthetically active tissues that participates in the formation of tropospheric ozone), contain a single  $C_5$  unit and are called hemiterpenes. More complex isoprenoids are usually formed by “head-to-tail” or “head-to-head” addition of isoprene units. Monoterpenes are  $C_{10}$  isoprenoids that consist of two isoprene units and are components of the essences of flowers, herbs, and spices. The isoprenoids that derive of three isoprene units are  $C_{15}$  sesquiterpenes, which can be found in essential oils and act as antimicrobial phytoalexins and antifeedants. The diterpenes ( $C_{20}$ ) include the side chain of chlorophyll, phylloquinones and tocopherol, gibberellins, phytoalexins, and taxol. The triterpenes ( $C_{30}$ ), such as phytosterols, brassinosteroids, and some phytoalexins, toxins, and waxes, are generated by the joining of two  $C_{15}$  chains. The most prevalent tetraterpenes ( $C_{40}$ ) are carotenoids, which are pigments in many flowers and fruits, contribute to light harvesting, and protect the photosynthetic apparatus from photooxidation. Polyterpenes contain more than eight isoprene units and include prenylated electron carriers (ubiquinone and plastoquinone) and polyprenols such as rubber and dolichol (required for protein glycosylation). The products of partial isoprenoid origin, including cytokinins or prenylated proteins, are called meroterpenes (McGarvey and Croteau, 1995; Croteau et al., 2000).

After the discovery of the mevalonic acid (MVA) pathway in yeast and animals in the 1950s, it was assumed that IPP was synthesized from acetyl-CoA via MVA and then isomerized to DMAPP in all organisms (Chappell, 1995; McGarvey and Croteau, 1995). In many cases, however, the experimental data on the biosynthesis of specific isoprenoids in plants and microorganisms could not be explained from the

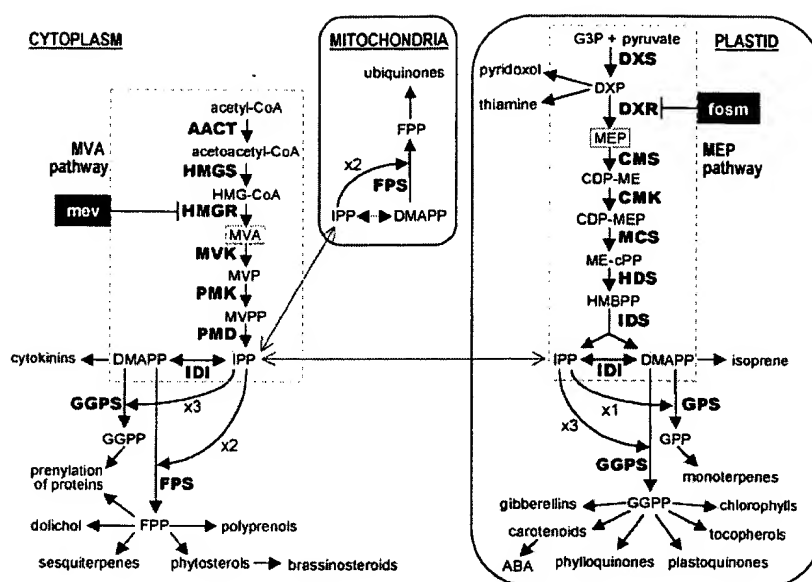
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**Figure 1.** Isoprenoid biosynthesis pathways in the plant cell. HMG-CoA, Hydroxymethylglutaryl CoA; MVP, 5-phosphomevalonate; MVPP, 5-diphosphomevalonate; HBMPP, hydroxymethylbutenyl 4-diphosphate; FPP, farnesyl diphosphate; ABA, abscisic acid. The first intermediate specific to each pathway is boxed. Enzymes are indicated in bold: **AACT**, acetoacetyl CoA thiolase (EC 2.3.1.9); **HMGs**, HMG-CoA synthase (EC 4.1.3.5); **HMGR**, HMG-CoA reductase (EC 1.1.1.88); **MVK**, MVA kinase (EC 2.7.1.36); **PMK**, MVP kinase (EC 2.7.4.2); **PMD**, MVPP decarboxylase (EC 4.1.1.33); **IDI**, IPP isomerase (EC 5.3.3.2); **GPS**, GPP synthase (EC 2.5.1.1); **FPS**, FPP synthase (EC 2.5.1.10); **GGPS**, GGPP synthase (EC 2.5.1.29); **DXS** (EC 4.1.3.37); **DXR**, DXP reductoisomerase (EC 1.1.1.267); **CMS** (EC 2.7.7.60); **CMK** (EC 2.7.1.148); **MCS** (EC 4.6.1.12); **HDS**; **IDS**, IPP/DMAPP synthase. The steps specifically inhibited by mevinolin (mev) and fosmidomycin (fosm) are indicated.



exclusive operation of the MVA pathway (for review, see Lichtenthaler et al., 1997, 1999; Eisenreich et al., 1998, 2001; Rohmer, 1999). A few years ago, an alternative MVA-independent pathway for the biosynthesis of the isoprene building units was identified by labeling experiments in bacteria (Flesch and Rohmer, 1988; Rohmer et al., 1993; Broers, 1994) and plants (Schwarz, 1994). This pathway was originally named non-mevalonate pathway or Rohmer pathway. After the identification of the first steps of the pathway, its name was changed to indicate the substrates (pyruvate/glyceraldehyde 3-phosphate [G3P] pathway) or the first intermediate, deoxyxylulose (DX) 5-phosphate (DXP pathway). However, it is becoming more accepted to name the pathway after what is currently considered its first committed precursor, methylerythritol 4-phosphate (MEP), following the same rule used to name the MVA pathway.

Isoprenoids are synthesized in all living organisms, but experimental evidence accumulated since the discovery of the MEP pathway has shown that most organisms only use one of the two pathways for the biosynthesis of their precursors. Thus, the MEP pathway is the only one present in most eubacteria and the malaria parasite *Plasmodium falciparum*, but it is absent from archaeobacteria, fungi and animals, which synthesize their isoprenoids exclusively through the operation of the MVA pathway. By contrast, plants use both the MEP pathway and the MVA pathway for isoprenoid biosynthesis, although they are localized in different compartments (Fig. 1; Lichtenthaler et al., 1997; Eisenreich et al., 1998, 2001; Lichtenthaler, 1999; Rohmer, 1999). The MEP pathway synthesizes IPP and DMAPP in plastids, whereas the MVA pathway produces cytosolic IPP (Fig. 1). Mitochondrial isoprenoids are synthesized from MVA-derived IPP that is imported from the cytosol (Lichtenthaler, 1999). Some exchange of IPP or a common down-

stream intermediate does also appear to take place between the plastids and the cytoplasm (for review, see Eisenreich et al., 1998, 2001; Lichtenthaler et al., 1997; Lichtenthaler, 1999; Rohmer, 1999). This limited exchange may explain in part why the MEP pathway was completely overlooked until very recently, because labeled precursors of the MVA pathway could be incorporated (although with very low efficiency) into most plastid isoprenoids. The now uncovered MEP pathway for the biosynthesis of isoprenoids may represent one of the last evolutionarily conserved metabolic pathways which remained to be unraveled.

#### SIMPLER IS BETTER. ELUCIDATION OF THE MEP PATHWAY IN *ESCHERICHIA COLI*

*E. coli*, the metabolically best studied bacterium, has served as a powerful model system for the elucidation of the MEP pathway (Fig. 2), which has been achieved thanks to multidisciplinary approaches that included organic chemistry, microbial genetics, biochemistry, molecular biology, and bioinformatics. However, the impressively fast identification of the genes involved in the pathway in bacteria and plants would not have been possible without recently developed genomic tools such as the availability of full genome sequences and expressed sequence tag (EST) collections. The elucidation of the MEP pathway is also a beautiful example of how genomics can be readily integrated with traditional approaches to identify whole metabolic pathways in distant organisms.

#### 1996 to 1998. From the Precursors to the Identification of the First Genes of the Pathway

Although evidences of a MVA-independent pathway for IPP biosynthesis were found independently

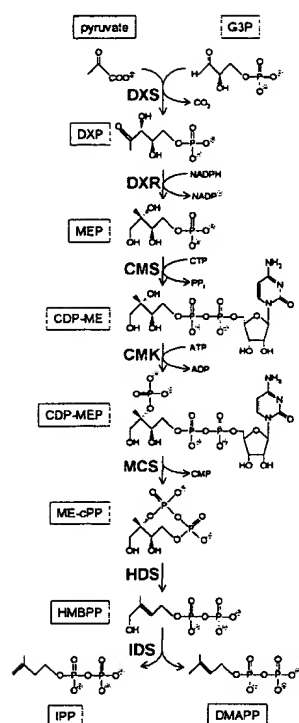


Figure 2. The MEP pathway. See Figure 1 for abbreviations.

by different research groups (Flesch and Rohmer, 1988; Rohmer et al., 1993; Broers, 1994; Schwarz, 1994), Rohmer and collaborators were the first in publishing their work in refereed journals. These authors used labeled precursors to study the biosynthesis of the bacterial isoprenoids hopanoids, and they observed labeling patterns that suggested the addition of a  $C_2$  unit derived from pyruvate by decarboxylation to a  $C_3$  triose phosphate (or a derivative) in a transketolase type reaction (Flesch and Rohmer, 1988; Rohmer et al., 1993). G3P and pyruvate were afterward identified as the direct precursors of IPP by labeling experiments with *E. coli* mutants defective in enzymes of the triose phosphate metabolism (Rohmer et al., 1996). These experiments suggested that the first reaction of the novel pathway involved the head-to-head condensation of (hydroxyethyl) thiamin derived from pyruvate with the C1 aldehyde group of G3P to yield DXP (Fig. 2), a compound that also serves as a precursor in the biosynthesis of the vitamins  $B_1$  (thiamine) and  $B_6$  (pyridoxol) in bacteria and plastids (Fig. 1). Other studies in different research groups confirmed the incorporation of labeled DX into bacterial and plant plastidial isoprenoids (for review, see Lichtenthaler et al., 1997; Eisenreich et al., 1998; Lichtenthaler, 1999; Rohmer, 1999).

Once this information was available, three independent approaches led to the identification of the first gene of the MEP pathway, encoding DXP synthase (DXS; Sprenger et al., 1997; Lange et al., 1998; Lois et al., 1998). Synthesis of DXP according to the mechanism described above required an acyloln con-

densation reaction whereby pyruvate is decarboxylated. This type of reaction was well documented as a secondary activity of thiamine diphosphate-dependent transketolases or the E1 component of pyruvate dehydrogenase or pyruvate decarboxylase. Taking advantage of the recent advent of full genomic sequence information for *E. coli*, Sprenger et al. (1997) and Lois et al. (1998) independently found a bacterial gene encoding a product with homology to transketolase and E1. Expression of the corresponding protein in *E. coli* and determination of its ability to form only DXP from pyruvate and G3P confirmed that it encoded a DXS enzyme (Sprenger et al., 1997; Lois et al., 1998). DXS-like sequences were found widespread in bacteria and plants but were absent from animal and yeast genomes. The Arabidopsis homolog had been previously described as CLA1, a plastid-targeted protein of unknown function encoded by a nuclear gene whose disruption caused an albino phenotype (Mandel et al., 1996). Following a homology-based approach, Lange et al. (1998) identified another plant transketolase-like sequence in a cDNA library from peppermint (*Mentha piperita*) oil gland secretory cells, which are highly specialized for monoterpene production and are therefore an enriched source of transcripts from genes involved in isoprenoid biosynthesis. The identified gene encoded a protein with DXS activity that was most similar to Arabidopsis CLA1, suggesting a role in the biosynthesis of plastid isoprenoids essential for photosynthesis and chloroplast function.

Rohmer et al. (1996) had proposed that an intramolecular rearrangement of DXP followed by an unspecified reduction process could produce MEP in the next reaction of the pathway (Fig. 2). Subsequent experiments showed that chemically synthesized ME was directly incorporated into *E. coli* isoprenoids (Duvold et al., 1997). A genetic strategy based on this information succeeded in identifying the bacterial gene encoding DXP reductoisomerase (DXR), the enzyme that converts DXP into MEP (Kuzuyama et al., 1998; Takahashi et al., 1998). Because MEP is only known to be a precursor for isoprenoids, these authors hypothesized that *E. coli* auxotrophic mutants requiring ME should be specifically affected in MEP and isoprenoid biosynthesis. After isolating mutants that grew on minimal medium with ME but not in the absence of this compound, they identified *yaeM* (now designated *dxr* or *ispC*) as the gene complementing ME auxotrophy in all the mutants and demonstrated that its product was a DXR enzyme involved in isoprenoid biosynthesis (Kuzuyama et al., 1998; Takahashi et al., 1998).

#### 1999 to 2000. Bioinformatics and Comparative Genomics Identify New Candidate Genes

For the identification of the next gene of the MEP pathway, Rohdich et al. (1999) incubated radiola-

beled MEP with *E. coli* cell extracts and purified enzyme fractions and observed that a radioactive product was produced when the reaction mixture contained a nucleotide 5'-triphosphate (CTP was the preferred substrate). On the basis of NMR spectroscopy data, the structure of the new metabolite was assigned as 4-diphosphocytidyl ME (CDP-ME; Fig. 2). A database search with CDP and pyrophosphorylase as keywords retrieved a gene encoding a bacterial enzyme that catalyzes the formation of CDP-ribitol from ribitol 5-phosphate and CTP. Subsequent database searches with this sequence uncovered a number of similar genes from organisms with the MEP pathway, including *Arabidopsis* (in which the corresponding protein encompassed a putative plastid leader sequence). Activity assays with the recombinant product of the *E. coli* gene (*ygbP*, also designated *ispD*) demonstrated that it encoded a CDP-ME synthase (CMS) that specifically produced CDP-ME from MEP and CTP (Fig. 2). Furthermore, incubation of radiolabeled CDP-ME with pepper (*Capsicum annuum*) chromoplasts resulted in the incorporation of radioactivity into carotenoids, suggesting that this metabolite was an intermediate of the MEP pathway (Rohdich et al., 1999).

The identification of the *E. coli* *dxs*, *dxr*, and *ygbP* genes provided sequence information that established the basis for a comparative genomics procedure that eventually led to the elucidation of the entire MEP pathway: the bioinformatic search for genes that were conserved in eubacteria and plants (the latter showing a N-terminal extension that could serve as a plastid targeting signal) but absent in archaeobacteria, yeast, and animals (which synthesize their isoprenoids exclusively from MVA). Thus, whole genome comparisons to identify genes after the distribution of the identified MEP pathway genes retrieved the next two genes of the MEP pathway, *ychB* and *ygbB*; Herz et al., 2000; Lüttgen et al., 2000). A procedure similar to that developed for *ygbP* was used to study the activity of the encoded proteins and their involvement in the MEP pathway. The purified recombinant enzyme encoded by the *E. coli* *ychB* gene was shown to be a CDP-ME kinase (CMK) that catalyzes the ATP-dependent phosphorylation of CDP-ME to CDP ME 2-phosphate (CDP-MEP). This compound was then converted into ME 2,4-cyclodiphosphate (ME-cPP) by the enzyme ME-cPP synthase (MCS), encoded by the *E. coli* *ygbB* gene (Fig. 2). As expected for MEP pathway enzymes, the plant homologs showed putative plastid signal peptides. In addition, incorporation experiments with pepper chromoplasts suggested that both CDP-MEP and ME-cPP were intermediates of the MEP pathway (Herz et al., 2000; Lüttgen et al., 2000). A plant gene homologous to *ychB* had previously been retrieved in a bioinformatic approach designed to identify ESTs encoding metabolite kinases in a cDNA library from peppermint oil gland secretory cells (Lange and Cro-

teau, 1999a). Although these authors proposed that the encoded protein could phosphorylate isopentenyl monophosphate to IPP in the putative last step of the MEP pathway, further experiments with the recombinant enzymes from *E. coli* and tomato (*Lycopersicon esculentum*) showed that they catalyzed the phosphorylation of CDP-ME to CDP-MEP at a much higher rate, indicating that this is the true metabolic role of the enzyme (Rohdich et al., 2000a).

#### 2000 to 2001. Strains Engineered to Synthesize IPP from MVA Demonstrate the Branching of the Pathway and Confirm the Role of the Previously Identified Genes

Although the results described above strongly suggested that *ygbP* (*ispD*), *ychB* (*ispE*), and *ygbB* (*ispF*) encoded enzymes directly involved in the MEP pathway, a clear-cut demonstration was provided by the development of a neat experimental system originally designed for the cloning of unknown MEP pathway genes in *E. coli* (Kuzuyama et al., 2000a, 2000b; Takagi et al., 2000; Campos et al., 2001a). To rescue lethal mutants in the MEP pathway genes, *E. coli* cells were genetically engineered with a recombinant MVA operon containing heterologous genes for the last three enzymes of the MVA pathway: MVA kinase, MVP kinase, and MVPP decarboxylase (see Fig. 1). These cells do not synthesize MVA, but they can take it from the growth medium and use it as an alternative source of IPP, which could be then converted to DMAPP by the *E. coli* IPP isomerase encoded by the *idi* gene (Hahn et al., 1999). By using this system Rodríguez-Concepción et al. (2000) demonstrated that *idi* is the only gene encoding an enzyme with IPP isomerase activity in *E. coli* and showed that this enzyme plays a role in isoprenoid biosynthesis in vivo. However, *idi* is not an essential gene in *E. coli* (Hahn et al., 1999; Rodríguez-Concepción et al., 2000). The work with strains harboring the MVA operon supported previous evidence from labeling experiments (Giner et al., 1998; Charon et al., 2000) demonstrating that the MEP pathway branched at some point after MEP leading to the separate synthesis of IPP and DMAPP (Rodríguez-Concepción et al., 2000). The MVA operon system was also used by two independent groups to provide genetic evidence that the enzymes encoded by *ygbP*, *ychB*, and *ygbB* catalyze reactions of the MEP pathway before the proposed branching, because the disruption of these genes was lethal, indicating that they were not acting in the proposed branches to IPP or DMAPP and could be rescued with MVA (Kuzuyama et al., 2000a, 2000b; Takagi et al., 2000; Campos et al., 2001a).

#### 2001 to 2002. Identification of the Last Two Genes of the Pathway

Although the described system with the MVA operon was a good genetic tool for the discovery of

the rest of the MEP pathway genes, they were first described by bioinformatic approaches of comparative genomics (Cunningham et al., 2000; Campos et al., 2001b). The *E. coli* genes annotated as *gcpE* (*ispG*) and *lytB* (*ispH*) were putatively ascribed to the MEP pathway because they were conserved in plants and eubacteria with this pathway but were absent from archaeobacteria, yeast, and animal genomes. In addition, the corresponding plant gene products contained an N-terminal domain that could act as a plastid targeting signal. Directed deletion of *gcpE* (Altincicek et al., 2001b; Campos et al., 2001b) or *lytB* (Altincicek et al., 2001a) in *E. coli* strains engineered with the MVA operon resulted in cells that were able to grow only when the medium was supplemented with MVA, demonstrating that both genes were required specifically for IPP biosynthesis in *E. coli*. Subsequent studies (Hecht et al., 2001; Seemann et al., 2002a, 2002b; Wolff et al., 2002) contributed to reveal that the *gcpE* gene product encoded an enzyme (hydroxymethylbutenyl 4-diphosphate [HMBPP] synthase [HDS]) that catalyzes the formation of HMBPP from ME-cPP (Fig. 2). The role of *lytB* is less clear, but it appears to encode an enzyme (IDS) that directly converts HMBPP into a 5:1 mixture of IPP and DMAPP (Fig. 2; Rohdich et al., 2002). Therefore, the activity of this enzyme could be identified as responsible for the branching, which had been previously predicted by biochemical and genetic approaches (Giner et al., 1998; Charon et al., 2000; Rodríguez-Concepción et al., 2000). The branching is an important difference with the MVA pathway, in which IPP and DMAPP are generated sequentially, the latter arising from the former in a reaction catalyzed by IPP isomerase (Fig. 1).

## THE MEP PATHWAY IN PLANTS

The recent development of genomic tools is revolutionizing the study of plant metabolism. As described above, the MEP pathway is a good example of how bioinformatics and comparative genomics have made relatively fast and simple to identify the

genes potentially involved in a metabolic pathway in different organisms based only on sequence information. Searches on The Arabidopsis Information Resources database (<http://www.Arabidopsis.org>) indicate that genes encoding proteins with homology to all the *E. coli* MEP pathway enzymes are present in Arabidopsis (Table I). The ChloroP algorithm (<http://www.cbs.dtu.dk/services/ChloroP>) predicts that all of these proteins contain a putative plastid targeting peptide of variable length (Table I), consistent with their predicted role in plastid isoprenoid biosynthesis. Functional genomics approaches consisting of the generation and screening of collections of T-DNA and transposon insertion mutants have led to the identification of Arabidopsis mutants defective in the genes encoding DXS, DXR, and CMS (Budziszewski et al., 2001). All of these mutants have a seedling-lethal albino phenotype, confirming that the MEP pathway is essential for plant life. With the increasing availability on public on-line databases of plant functional genomics tools (including collections of ESTs and DNA microarrays), it will soon become possible to even deduce accurate gene expression data that may provide some clues as to their biological role. However, only functional analysis of each proposed plant protein ortholog with biochemical and genetic approaches will ascertain its contribution to the biosynthesis of plastid isoprenoids.

## Plant Genes and Enzymes

Genes and ESTs corresponding to all the MEP pathway enzymes (Table I) can be found in the available Arabidopsis databases. The most abundant ESTs are those from the genes encoding DXS and HDS (about 0.2% of all the ESTs in the collections), followed by IDS (0.1%). These ESTs are widely distributed in the available Arabidopsis collections (which are made from a variety of tissues and developmental stages) suggesting that the corresponding genes are expressed throughout the plant. From all of the tentative orthologs of the *E. coli* MEP pathway enzymes that can be found in the Arabidopsis genome,

**Table I.** Arabidopsis MEP pathway proteins

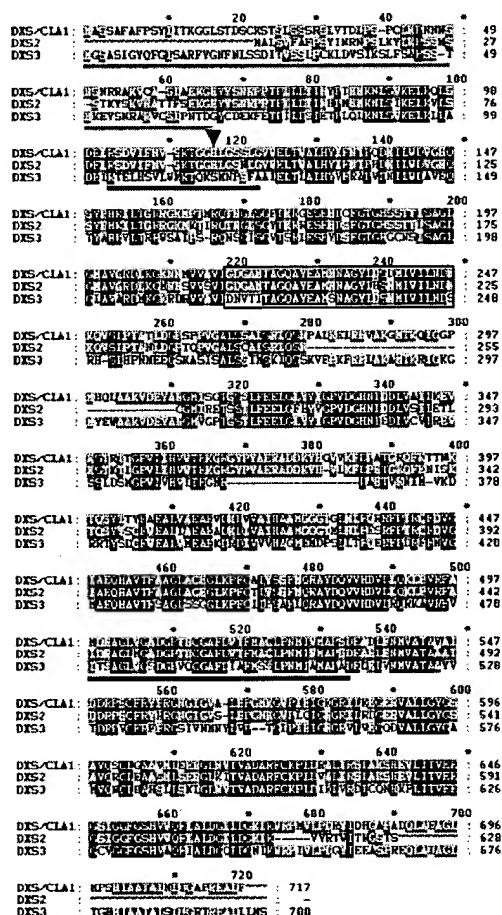
The enzymes that have been demonstrated to be involved in plastid isoprenoid biosynthesis are shown in bold. The length of the proteins and their predicted plastid targeting peptides (PTP) is indicated with the number of amino acid residues. The total number of ESTs in GenBank Arabidopsis collections (113,330 ESTs) is also shown.

Protein	Other Names	Accession No.	Length (PTP)	ESTs
<b>DXS</b>	CLA1	At4g15560	717 (58)	23
DXS2		At3g21500	628 (35)	3
DXS3		At5g11380	700 (47)	1
<b>DXR</b>	ISPC,YAEM	At5g62790	477 (49)	4
<b>CMS</b>	ISPD,YGBP	At2g02500	302 (61)	1
<b>CMK</b>	ISPE,YCHB	At2g26930	383 (41)	6
MCS	ISPF,YGBB	At1g63970	223 (52)	4
<b>HDS</b>	ISPC,GCPE	At5g60600	740 (38)	24
<b>IDS</b>	ISPH,LYTB	At4g34350	452 (38)	13

only DXS might be encoded by more than one gene (Table I). Arabidopsis *cla1* mutants defective in DXS (At4g15560) show an albino phenotype and a very early arrest of chloroplast development that can be rescued with DX (Mandel et al., 1996; Araki et al., 2000; Estévez et al., 2000). However, mutant plants can still accumulate low levels of plastid isoprenoids such as chlorophylls and carotenoids, suggesting either an import of cytosolic MVA-derived isoprenoid precursors to the plastids or the presence of extra DXS enzymes (Araki et al., 2000; Estévez et al., 2000). Two other Arabidopsis proteins, predicted from genomic and EST sequences and tentatively named DXS2 (At3g21500) and DXS3 (At5g11380), show homology to DXS (Fig. 3). Only a few ESTs from these genes have been found in green siliques (three ESTs

from DXS2) and roots (one EST from DXS3), suggesting that their expression is low and may be restricted to certain tissues or developmental stages. By contrast, the gene encoding DXS is widely expressed in the Arabidopsis plant, as deduced from the number and distribution of ESTs (Table I) and the analysis of mRNA and protein accumulation (Estévez et al., 2000). The differential expression pattern could explain why DXS-deficient seedlings show a block in plastid isoprenoid synthesis (which causes the albino phenotype) that is not rescued by the other two putative DXS isoforms. Although both DXS2 and DXS3 contain N-terminal sequences predicted by the ChloroP program to target them to plastids (Table I; Fig. 3), it is not known whether they are functional DXS enzymes with a role in the MEP pathway. The deduced mature proteins lack stretches of amino acids that are present in all the bacterial and plant DXS enzymes (Lois et al., 1998, 2000), and a conserved His residue essential for DXS activity (Querol et al., 2001) is not present in the DXS3 protein (Fig. 3). A functional analysis is therefore needed to confirm the predictions generated by the sequence-based analysis and to demonstrate their biological function.

The rest of the Arabidopsis MEP pathway enzymes (Table I) appear to be encoded by a single gene, and functional data supporting their role in plastid isoprenoid biosynthesis are available for DXR (Lange and Croteau, 1999b; Schwender et al., 1999; Carretero-Paulet et al., 2002), CMS (Rohdich et al., 2000b; Okada et al., 2002), and HDS (Querol et al., 2002). A CMK ortholog from tomato has also been described (Rohdich et al., 2000a). The most obvious difference between plant and *E. coli* MEP pathway enzymes is the presence of N-terminal extensions of variable sequence and length (Table I), which have been shown to function as plastidial signal peptides for plant DXS (Araki et al., 2000; Lois et al., 2000), DXR (Rodríguez-Concepción et al., 2001; Carretero-Paulet et al., 2002), and HDS (Querol et al., 2002). The mature proteins produced after cleavage of these peptides are similar to the bacterial enzymes except in the case of HDS (GCPE), which contains a large plant-specific domain (Querol et al., 2002). The mature Arabidopsis HDS protein is able to complement the lethal deletion of the *gcpE* gene in *E. coli*, but it is possible that because of this extra domain, the plant protein may have distinct regulatory or catalytic functions. Most of the work on the characterization of the MEP pathway enzymes has been done with the *E. coli* proteins, including the resolution of the crystal structure of the enzymes DXR (Reuter et al., 2002; Yajima et al., 2002), CMS (Kemp et al., 2001; Richard et al., 2001), and MCS (Kemp et al., 2002; Richard et al., 2002; Steinbacher et al., 2002). By contrast, only limited knowledge about the catalytic properties of the plant enzymes is available (for review, see Eisenreich et al., 2001).



**Figure 3.** Multiple alignment of Arabidopsis DXS-like proteins. Sequences from Arabidopsis DXS (At4g15560), DXS2 (At3g21500), and DXS3 (At5g11380) were aligned using the ClustalW program (<http://www2.ebi.ac.uk/clustalw>). Identical residues are highlighted in black boxes (when present in all three sequences) or gray boxes (those only present in two sequences). The N-terminal region absent from bacterial DXS proteins is underlined in gray. Sequence signatures of transketolase and DXS enzymes (Querol et al., 2001) include the thiamine diphosphate-binding domain (boxed) and two other conserved motifs (black bar), one of which contains a His residue required for activity (arrowhead).

### Regulation of the Metabolic Flow through the MEP Pathway

Despite the impressive progress in the elucidation of the MEP pathway in bacteria and plants, much work is still ahead to analyze the contribution of the different enzymes to the control of the flux of intermediates through the pathway that will eventually determine the supply of IPP and DMAPP for the synthesis of plastid isoprenoid end products. The first studies have been carried out with DXS and DXR (Mandel et al., 1996; Bouvier et al., 1998; Lange et al., 1998; Lange and Croteau, 1999b; Schwender et al., 1999; Araki et al., 2000; Chahed et al., 2000; Estévez et al., 2000, 2001; Lois et al., 2000; Veau et al., 2000; Walter et al., 2000; Mahmoud and Croteau, 2001; Rodríguez-Concepción et al., 2001; Carretero-Paulet et al., 2002). To date, DXS is the only enzyme of the MEP pathway that has been shown to have a limiting role for isoprenoid biosynthesis in all the systems analyzed, including *Arabidopsis* (Estévez et al., 2001), tomato (Lois et al., 2000), and bacteria (Harker and Bramley, 1999; Miller et al., 1999, 2000; Kuzuyama et al., 2000c; Matthews and Wurtzel, 2000). The role of DXR is less clear. Overexpression studies suggest that DXR activity is not limiting for isoprenoid biosynthesis in bacteria (Miller et al., 2000). The dramatic accumulation of carotenoids that takes place during tomato fruit ripening does not require increased levels of DXR transcripts and encoded protein either (Rodríguez-Concepción et al., 2001). By contrast, overexpression of DXR in peppermint led to increased isoprenoid synthesis (Mahmoud and Croteau, 2001), and a positive correlation was found between enhanced isoprenoid biosynthesis and accumulation of transcripts encoding both DXS and DXR in monocot roots (Walter et al., 2000) and periwinkle (*Catharanthus roseus*) cell cultures (Veau et al., 2000). The distribution of DXR and DXS transcripts in the *Arabidopsis* plant is similar, with highest levels in light-grown seedlings and inflorescences (Carretero-Paulet et al., 2002). However, DXS expression precedes that of DXR in some organs, such as developing inflorescences, suggesting that DXR instead of DXS might be limiting for the onset of plastid isoprenoid biosynthesis in this case (Carretero-Paulet et al., 2002). Together, the results support a general regulatory role for DXS in controlling the metabolic flux through the MEP pathway, whereas DXR activity may be limiting or not depending on the species, organ, and/or developmental stage. It is likely that other enzymes of the MEP pathway may also contribute to regulate the supply of intermediates for plastid isoprenoid biosynthesis, but this remains to be established.

### Coordination with Related Metabolic Pathways

The MEP pathway produces plastidial IPP and DMAPP precursors that are then used as building

blocks for the production of isoprenoid end products by many different pathways (Fig. 1). A central question is how the downstream pathways are coordinated with the MEP pathway (and among them) to make sure that the required precursors will be supplied when needed. Expression of some of the MEP pathway genes has been shown to either precede or parallel the activation of specific pathways for the production of monoterpenes in peppermint oil gland secretory cells (Lange et al., 1998), monoterpenoid indole alkaloids in periwinkle cell cultures (Veau et al., 2000), apocarotenoids in monocot roots (Walter et al., 2000), and carotenoids in pepper and tomato fruit (Bouvier et al., 1998; Lois et al., 2000). In the last case, it has been shown that the expression of tomato DXS can be regulated by changes in the carotenoid composition of the fruit (Lois et al., 2000). Furthermore, changes in the levels of MEP pathway intermediates in tomato fruit fed with DX or treated with fosmidomycin (a specific inhibitor of DXR activity; Fig. 1) induced the expression of DXS but also of *PSY1*, the gene encoding the committed enzyme that catalyzes the first step of the carotenoid pathway in fruit (Lois et al., 2000; Rodríguez-Concepción et al., 2001). These results suggest a significant coordination between both the MEP pathway and the carotenoid pathway through the control of the expression of key genes, which may contribute to a fine regulation of carotenoid accumulation. Interference with this balanced regulation by overexpression of *PSY1* under the 35S promoter in transgenic tomato led to the production of dwarf plants because the geranylgeranyl diphosphate available for gibberellin synthesis was redirected into the carotenoid pathway (see Fig. 1; Fray et al., 1995). This exemplifies how our limited knowledge on the mechanisms by which the MEP pathway and the downstream pathways are coordinated represents an important obstacle to modify precisely the production of specific isoprenoid end products.

The unique compartmentalization of isoprenoid biosynthesis in plants involves the existence of additional plant-specific regulatory mechanisms. Although the MEP pathway and the MVA pathway are independent pathways that are physically separated, they usually coexist within the plant cell (Fig. 1). In fact, a limited exchange of isoprene building units (IPP and DMAPP) or a common downstream intermediate takes place between compartments, and some isoprenoid end products are built from precursors supplied by both the MEP pathway and the MVA pathway (for review, see Eisenreich et al., 1998, 2001; Lichtenthaler et al., 1997; Lichtenthaler, 1999; Rohmer, 1999). Although the extent of this crossflow depends on the plant species, it has been estimated to be below 1% in intact plants under physiological conditions (Eisenreich et al., 2001). In experiments carried out with seedlings, the rate of exchange of intermediates appears not to be high enough to fully rescue a block of one of the two pathways. Thus, the



specific inhibition of MVA-derived isoprenoid biosynthesis with mevinolin (Fig. 1) in radish (*Raphanus sativus*) seedlings cannot be overcome by the delivery of common isoprenoid intermediates from the plastidial MEP pathway (Schindler et al., 1985). Arabidopsis mutant seedlings defective in MEP pathway genes (Mandel et al., 1996; Araki et al., 2000; Estévez et al., 2000; Budziszewski et al., 2001) similarly show an albino phenotype likely because the block in the synthesis of plastid isoprenoids required for photosynthesis and photoprotection (such as chlorophylls, carotenoids, tocopherol, and plastoquinone) cannot be rescued by the import of cytosolic MVA-derived intermediates. The same phenotype is observed when seeds from Arabidopsis (Fig. 4) or tomato (Rodríguez-Concepción et al., 2001) are germinated in the presence of fosmidomycin, a specific DXR inhibitor that causes a general block in plastid isoprenoid biosynthesis (Zeidler et al., 1998). However, the dynamics and the regulation of the crossflow of common intermediates between cell compartments may vary dramatically in different species, cell types, and/or developmental stages. This is an area of intensive research that will benefit from the availability of specific inhibitors such as mevinolin and fosmidomycin (Fig. 1) to block any of the two pathways for

isoprenoid synthesis in a given plant, organ, or stage of development. For instance, treatment of tomato mature green fruit with fosmidomycin inhibited subsequent carotenoid accumulation (Zeidler et al., 1998; Rodríguez-Concepción et al., 2001), resulting in fruit of yellow-orange color instead of red when ripe (Fig. 4C). These results and previous experiments of treatment with mevinolin (Rodríguez-Concepción and Gruissem, 1999) support that the MVA pathway does not contribute significantly to carotenoid biosynthesis in tomato fruit. Future experiments should establish how the crossflow of MEP- or MVA-derived isoprenoid intermediates is modulated under physiological conditions and the nature of the transport system for prenyl diphosphate compounds between cytoplasm and plastids.

## CONCLUDING REMARKS

The joint contribution of genomics integrated with traditional biochemical and genetic approaches has led to the impressively fast elucidation of the MEP pathway for the biosynthesis of plastid isoprenoids, a metabolic milestone that represents a huge step forward toward understanding (and manipulating) isoprenoid biosynthesis in plants. Nevertheless, we still lack fundamental knowledge on the regulatory mechanisms that control the flow of intermediates through the pathway and the coordination with related metabolic pathways. The benefits that the characterization of the MEP pathway can represent go beyond metabolic engineering. The MEP pathway, which is absent from humans but is present in pathogenic bacteria (many of which are acquiring resistance to currently available antibiotics) and in the malaria parasite *Plasmodium falciparum*, constitutes an ideal target for the development of novel antimalarial and antibacterial agents (Jomaa et al., 1999; Altincicek et al., 2001c; Hintz et al., 2001). Plants are promising test systems for the development of such inhibitors of the MEP pathway, which could also serve as herbicides (Zeidler et al., 2000; Lange et al., 2001).

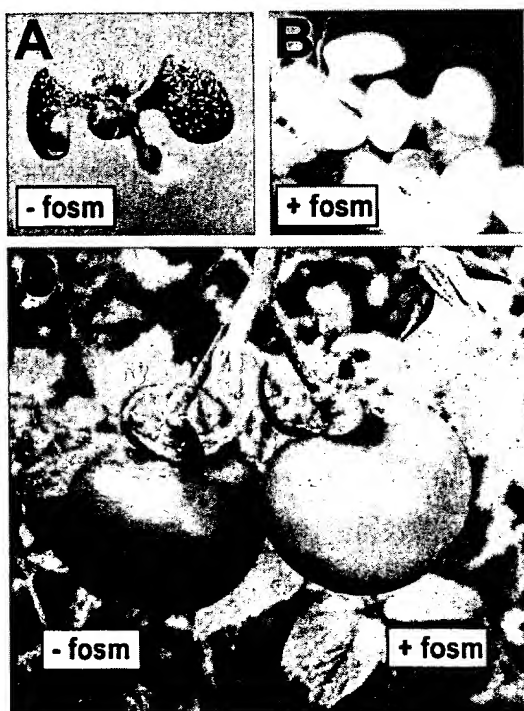
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**Figure 4.** Inhibition of plastid isoprenoid biosynthesis with fosmidomycin (fosm). A, Arabidopsis seedling grown for 10 d on Murashige and Skoog medium. B, Arabidopsis seedlings grown for 10 d on Murashige and Skoog medium supplemented with 100  $\mu$ M fosmidomycin. C, Tomato fruit 2 weeks after injection at the mature green stage with a 10 mM Tris, pH 8.5, solution (left fruit) or the same solution containing fosmidomycin to a final concentration of 200  $\mu$ M (right fruit). Fruit volume was estimated from the diameter.

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# Metabolic engineering of essential oil yield and composition in mint by altering expression of deoxyxylulose phosphate reductoisomerase and menthofuran synthase

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Peppermint (*Mentha × piperita* L.) was independently transformed with a homologous sense version of the 1-deoxy-D-xylulose-5-phosphate reductoisomerase cDNA and with a homologous antisense version of the menthofuran synthase cDNA, both driven by the CaMV 35S promoter. Two groups of transgenic plants were regenerated in the reductoisomerase experiments, one of which remained normal in appearance and development; another was deficient in chlorophyll production and grew slowly. Transgenic plants of normal appearance and growth habit expressed the reductoisomerase transgene strongly and constitutively, as determined by RNA blot analysis and direct enzyme assay, and these plants accumulated substantially more essential oil (about 50% yield increase) without change in monoterpene composition compared with wild-type. Chlorophyll-deficient plants did not afford detectable reductoisomerase mRNA or enzyme activity and yielded less essential oil than did wild-type plants, indicating cosuppression of the reductoisomerase gene. Plants transformed with the antisense version of the menthofuran synthase cDNA were normal in appearance but produced less than half of this undesirable monoterpene oil component than did wild-type mint grown under unstressed or stressed conditions. These experiments demonstrate that essential oil quantity and quality can be regulated by metabolic engineering. Thus, alteration of the committed step of the mevalonate-independent pathway for supply of terpenoid precursors improves flux through the pathway that leads to increased monoterpene production, and antisense manipulation of a selected downstream monoterpene biosynthetic step leads to improved oil composition.

peppermint | *Mentha × piperita* | monoterpene biosynthesis | mevalonate-independent pathway | isoprenoids

Isoprenoids are a large and structurally diverse family of compounds that play essential roles in plants as hormones, photosynthetic pigments, electron carriers, and membrane components and that also serve in communication and defense (1). Although isoprenoids are universally synthesized through condensations of the five-carbon compound isopentenyl diphosphate (IPP) and its allylic isomer dimethylallyl diphosphate (DMAPP), two distinct and independent biosynthetic routes to these precursors exist in plants. The cytosolic pathway to IPP (Fig. 1A) starts from acetyl-CoA and proceeds through the classical intermediate mevalonic acid to provide precursors for the biosynthesis of sesquiterpenes (C<sub>15</sub>) and triterpenes (C<sub>30</sub>) (2). The plastidial pathway (Fig. 1B) is initiated by the transketolase-type condensation of pyruvate (carbons 2 and 3) and glyceraldehyde-3-phosphate to 1-deoxyxylulose-5-phosphate (DXP), followed by the isomerization and reduction of this intermediate to 2-C-methylerythritol-4-phosphate, formation of the cytidine 5'-diphosphate derivative, phosphorylation at C2, and cyclization to 2-C-methylerythritol-2,4-cyclodiphosphate as the last defined step (3–6). This plastidial pathway provides precursors

for the biosynthesis of isoprene (C<sub>5</sub>), monoterpenes (C<sub>10</sub>), diterpenes (C<sub>20</sub>), and tetraterpenes (C<sub>40</sub>) (4, 7), and genes encoding each enzyme of the pathway, up to formation of the cyclic diphosphate, have been isolated from plants and from eubacteria in which the pathway also operates (8–19).

Transgenic manipulations of the mevalonate-independent (DXP) pathway in *Escherichia coli* have indicated that IPP and DMAPP likely arise independently by branching of the pathway (20) and that overexpression of the first pathway gene, for DXP synthase (DXPS), increases carotenoid and ubiquinone biosynthesis (21, 22); manipulation of the mevalonate pathway that operates in yeast also results in increased carotenoid production (23). Studies on the results of overexpression and underexpression of DXPS in *Arabidopsis* have recently indicated that this enzyme catalyzes a slow step in the mevalonate-independent pathway to plastidial isoprenoids (chlorophylls and carotenoids) (24), and considerable literature exists on the transgenic alteration of hydroxymethylglutaryl CoA reductase in plants and the influence on cytosolic isoprenoid production (sesquiterpene phytoalexins and phytosterols); however, the roles of the various reductase isoforms in differentially regulating the mevalonate pathway are not fully clear (25–28). The control of flux through each pathway of isoprenoid biosynthesis in plants, in which both mevalonate and mevalonate-independent (DXP) pathways operate, and the level and means of interaction between the two pathways are of considerable interest in the context of both primary and secondary plant metabolism.

Monoterpenes comprise the major components of the essential oils of the mint family (Lamiaceae), including peppermint (*Mentha × piperita*), which has been developed as a model system for the study of monoterpene metabolism. Peppermint oil is chemically complex, and the biosynthetic pathway leading to the major monoterpene component (–)-menthol (Fig. 2) involves a broad range of representative reaction types of terpenoid metabolism (e.g., cyclization, hydroxylation, redox transformations) (29). Monoterpene biosynthesis in mint is specifically localized to the glandular trichomes (30) and originates in the leucoplasts of the secretory cells of these highly specialized nonphotosynthetic epidermal structures (31). During the brief but intense period of secretory activity (32, 33), monoterpene biosynthesis is driven by plastidial supply of IPP and DMAPP via the DXP pathway; the cytosolic mevalonate pathway is also inactive at this stage of oil gland development (34). It is of interest to determine whether flux through the mevalonate-independent pathway is

Abbreviations: DMAPP, dimethylallyl diphosphate; DXP(S), deoxyxylulose phosphate (synthase); DXR, DXP reductoisomerase; IPP, isopentenyl diphosphate; MFS, menthofuran synthase; NPT, neomycin phosphotransferase; WT, wild type.

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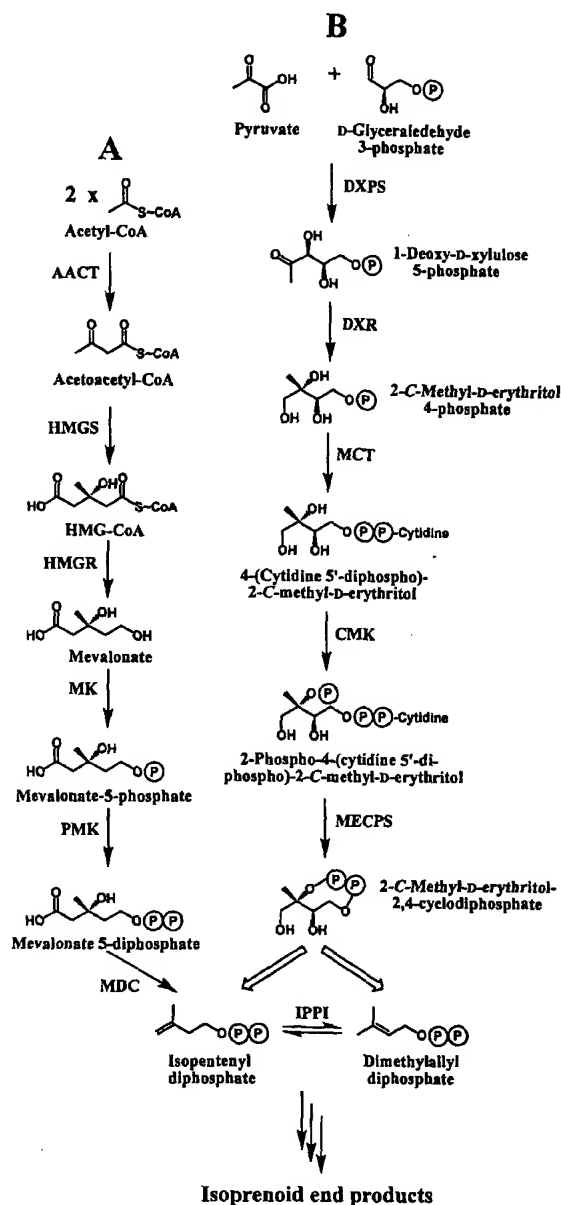


Fig. 1. Biosynthesis of IPP and DMAPP via the mevalonate pathway (A) and the mevalonate-independent (DXP) pathway (B). The indicated enzymes are: AACT, acetyl-CoA/acetyl-CoA C-acetyltransferase; HMGS, 3-hydroxy-3-methylglutaryl-CoA synthase; HMGR, 3-hydroxy-3-methylglutaryl-CoA reductase; MK, mevalonate kinase; PMK, phosphomevalonate kinase; MDC, mevalonate-5-diphosphate decarboxylase; DXPS, 1-deoxyxylulose-5-phosphate synthase; DXR, 1-deoxyxylulose-5-phosphate reductoisomerase; MCT, 2-C-methylerythritol-4-phosphate (MEP) cytidyltransferase; CMK, 4-(cytidine 5'-diphospho)-2-C-methylerythritol kinase; MECPS, 2-C-methylerythritol-2,4-cyclodiphosphate synthase; and IPP isomerase (IPPI). The circled P denotes the phosphate moiety. The large open arrows indicate several as-yet-unidentified steps. The pathway may give rise to IPP and DMAPP independently (20) of the interconversion catalyzed by IPPI.

limiting during the period of very rapid terpenoid biosynthesis by manipulating this route for precursor supply. Such a finding could have important implications for production of the essential oils and other terpenoids of commercial significance (35).

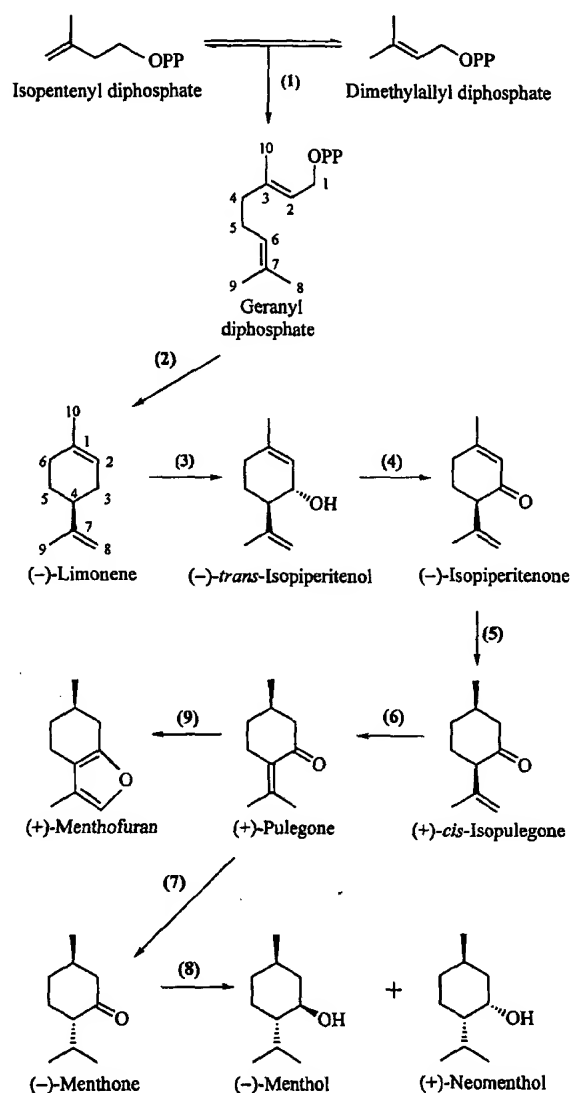


Fig. 2. The principal pathway for monoterpene biosynthesis in peppermint. The responsible enzymes are: 1) geranyl diphosphate synthase; 2) (-)-limonene synthase; 3) cytochrome P450 (-)-limonene-3-hydroxylase; 4) (-)-trans-isopiperitenol dehydrogenase; 5) (-)-isopiperitenone reductase; 6) (+)-cis-isopulegone isomerase; 7) (+)-pulegone reductase; 8) (-)-menthone reductase; and 9) cytochrome P450 (+)-MFS. The circled P denotes the phosphate moiety.

Because DXP is an intermediate not only for IPP and DMAPP biosynthesis but also for the biosynthesis of thiamin and pyridoxol (36, 37), it is the conversion of DXP to methylerythritol phosphate (Fig. 1B), catalyzed by DXP reductoisomerase (DXR) (11), that represents the committed step in the production of IPP. In this paper, we report the transformation of peppermint with the homologous cDNA for DXR (12) under the control of a strong constitutive promoter and describe the influence of modified expression of this gene on essential oil production yield and mint physiology.

(+)-Menthofuran is an undesirable monoterpene component of peppermint that is derived from the  $\alpha,\beta$ -unsaturated ketone (+)-pulegone (38) (Fig. 2); it contributes off-flavor to the isolated essential oil and promotes off-color on storage (39, 40).

The content of menthofuran can reach industrially unacceptable levels in plants raised under stressful environmental conditions (high temperature, drought, low light intensity) (41, 42), over which commercial mint growers have very limited control. A cDNA-encoding cytochrome P450 (+)-menthofuran synthase (MFS) [(+)-pulegone-9-hydroxylase] was recently isolated from peppermint (38), thus offering a direct, but heretofore unexplored, means for transgenic manipulation of menthofuran production. In this paper, we also report the transformation of peppermint with the antisense version of (+)-MFS (38) under the control of a strong constitutive promoter, and we describe the influence of decreased expression of this gene on the composition of the essential oil produced in stressed and unstressed plants.

## Materials and Methods

**Plant Material.** Peppermint plants (the sterile hybrid *Mentha × piperita* L. cv. Black Mitcham) were propagated from rhizomes and stem cuttings in flats containing peat moss/pumice/sand (55:35:10, vol/vol/vol) and were grown under controlled conditions at 500–600  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  photosynthetically active radiation at plant height, with a 16-h photoperiod and a 26°C/15°C (day/night) temperature cycle (43). To induce moderate stress, which alters oil composition by increasing the levels of (+)-menthofuran and (+)-pulegone (41, 42), the photon flux density was reduced to 200–300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and the night temperature was increased to 21°C. All plants were watered and fertilized daily with a complete fertilizer (N/P/K, 20:20:20) plus iron chelate and micronutrients, and all flats were grown to complete confluence, then pruned and regrown to maturity (preflowering) before harvesting for oil analysis.

**Vector Assembly and Plant Transformation.** The parent vector pGAdexG/Nuclear Inclusion-b protein (Nlb).L was provided by J. C. Carrington of the Institute of Biological Chemistry. This vector is derived from pGA482 (44) and contains a  $\beta$ -glucuronidase (GUS)-Nlb gene fusion inserted between the CaMV tandem 35S promoter with duplicated enhancer and the *Agrobacterium* NOS transcriptional terminator. The GUS-Nlb fusion was excised with *EcoRI*/*KpnI* and replaced by ligation with the DXR cDNA, which was amplified from the original clone (12) by using forward primer (5'-ACTGTCGAATTCATGGCTCTAAACTTGATGGC-3') and reverse primer (5'-ATCGCTGGTACCGCTCATACAAGAGCAGGAC-3') to introduce the respective 5'-*EcoRI* site upstream of the start codon and 3'-*KpnI* site downstream of the stop codon. The coding region (antisense version) of the MFS cDNA (38) was amplified by PCR by using primers (5'-CGCCGCGAATTCTCAAGATTGACGTGGAGTAGC-3') and (5'-CGCCGCGGTACCATGGCCGCTCTTCTAG-3') to generate an *EcoRI* site and a *KpnI* site at the respective 3'- and 5'-termini of the gene. The resulting gel-purified amplicon was digested with *EcoRI* and *KpnI* and ligated into similarly prepared and gel purified pGAdexG/Nlb.L to replace the original GUS-Nlb insert as before.

The sequence-verified constructs were electroporated into *Agrobacterium tumefaciens* strain EHA105 by using the MicroPulser (Bio-Rad) according to the manufacturer's protocol. A single transformant bearing each construct was isolated and grown to log phase in minimal medium (45) containing 50 mg of kanamycin  $\text{L}^{-1}$  and 30 mg of rifampicin  $\text{L}^{-1}$ , harvested by centrifugation, resuspended in minimal medium containing 0.2 mM acetosyringone, and used to infect peppermint leaf discs as previously described (46, 47). After regeneration by established protocols (46, 47), rooted plantlets were transferred to soil, acclimated, and then moved to the greenhouse and propagated as above.

**RNA Isolation and Blot Analysis.** Total RNA was extracted from immature (1–2 cm) and fully expanded (>4 cm) peppermint leaves by using the Trizol Reagent (GIBCO/BRL) according to the supplier's protocol. Ten micrograms of denatured RNA was separated by electrophoresis on a 1.2% agarose-formaldehyde gel and transferred to a Hybond-N nylon membrane (Amersham Pharmacia) by standard protocol (48).  $^{32}\text{P}$ -labeled DNA probe, prepared by random priming of the cDNA encoding DXR, was used to detect the corresponding mRNA. Prehybridization was conducted at 65°C for 1 h in 0.5 ml/cm<sup>2</sup> of Rapid Hyb buffer (Amersham Pharmacia), followed by hybridization with the  $^{32}\text{P}$ -labeled probe ( $8 \times 10^6$  cpm) under the same conditions for 2 h, and then washing in 4× (15 min, room temperature), 2× (15 min, 65°C), and 1× (15 min, 65°C) SSC containing 0.1% SDS before exposure to Kodak X-Omat x-ray film overnight.

**Enzyme Isolation and Assay.** Soluble enzyme extracts from peppermint leaves (2–3 cm in length, 0.5 g) were prepared by a standard procedure (49). The resulting soluble enzyme fraction (8 ml) was then suspended with ceramic hydroxyapatite (Bio-Rad, 2 g matrix/8 ml extract) that had been prewashed and equilibrated with extraction buffer [20 mM potassium phosphate (pH 6.5)/10 mM sodium ascorbate/10 mM  $\text{MgCl}_2$ /1 mM DTT]. The slurry was gently mixed for 1 h at 0–4°C to allow protein adsorption, and the matrix was then removed by centrifugation to provide a supernatant essentially free of phosphatase activity that interferes with the DXR assay and neomycin phosphotransferase (NPT) assay. The NPT assay followed an established literature procedure (50). The preparation of the substrate [ $^{14}\text{C}$ ]DXP and the details of the radio-HPLC-based assay for DXR activity have been previously described (12).

**Essential Oil Analysis.** Confluent flats of transgenic mint or wild-type (WT) controls were grown to maturity (flower bud stage) and were individually harvested and frozen at –20°C. The frozen tissue was then manually crushed and mixed to ensure sample uniformity, and three 10-gram samples from each trial (large-stem fragments were excluded) were taken for simultaneous steam distillation–pentane extraction as previously described (43) by using (+)-camphor as an internal standard. One-microliter aliquots of the diluted distillate were analyzed for terpenoid content by gas chromatography (and coupled gas chromatography–mass spectrometry) as described elsewhere (43), and the products were quantified (in milligram/gram tissue fresh weight) by comparison of detector response with that of the internal standard.

## Results and Discussion

The first step of the plastidial mevalonate-independent pathway for the production of isoprenoid precursors is catalyzed by DXPS (5, 6), which also supplies precursor (DXP; see Fig. 1) for the synthesis of thiamin and pyridoxol (36, 37). The second step of the pathway is catalyzed by DXR (for the conversion of DXP to methylerythritol phosphate; see Fig. 1), which is considered the committed step in the supply of terpenoid precursors (11) and thus a potential target for control of flux through this branch of the pathway. There have been no previous attempts to manipulate DXR or to evaluate the influence of this or any other gene of the mevalonate-independent pathway on the production yield of essential oil terpenes. A cDNA encoding DXR was isolated from peppermint (12); this 1,425-nt sequence encodes a preprotein bearing an N-terminal plastidial peptide that directs the enzyme to the plastids where the mevalonate-independent pathway operates. The mature enzyme comprises about 400 amino acid residues with a size of about 43.5 kDa, and it resembles other reductoisomerases of plant and eubacterial origin (51).

(+)-MFS was recently demonstrated to be a cytochrome P450 enzyme capable of hydroxylating the *syn* (C9)-methyl group of

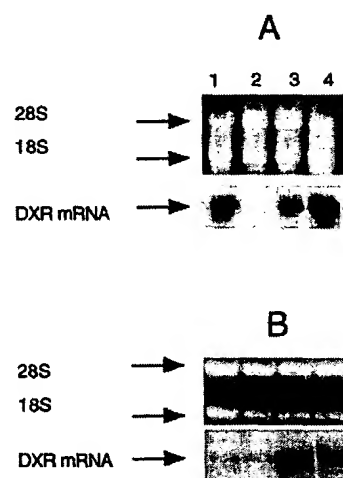
(+)-pulegone, which leads to spontaneous intramolecular cyclization to the hemiketal and dehydration to the furan, to yield this commercially undesirable essential oil component (38). An abundant cytochrome P450 clone from a peppermint oil gland cell cDNA library (52) was functionally expressed in *Saccharomyces cerevisiae* and *E. coli* and shown to encode MFS (38), thus offering a transgenic means for control of menthofuran production. The full-length cDNA contains 1,479 nucleotides and encodes a protein of 493-aa residues of molecular weight 55,360, which bears a typical N-terminal membrane insertion sequence and all of the anticipated primary structural elements of a cytochrome P450.

**Preparation and Evaluation of Transformed Plants.** Genetic transformation of peppermint was accomplished by an established protocol by using *A. tumefaciens* strain EHA105 (46, 47) and a binary vector pGA482 (44) containing *npt* and the full-length (sense) *dxr* construct (12) or the resistance gene and the antisense version of *mfs* (38). Subsequent regeneration and selection from leaf disks transformed with the sense version of *dxr* yielded 57 kanamycin-resistant plants, and of leaf disks transformed with the antisense version of *mfs* yielded 19 kanamycin-resistant plants. Gene transfer in both cases was confirmed directly by assay of leaf extracts for expression of the selectable marker (*npt*) (50), and all NPT-positive plants were propagated for further analysis.

All 19 of the verified transformants bearing the antisense MFS cDNA and most transgenic plants transformed with the DXR (sense) cDNA (42 plants designated the TI group) were indistinguishable from WT plants. In the population of *dxr* transformants, 11 plants (designated the TIIA group) did not develop normal pigmentation; instead, the leaves appeared uniformly lighter green, suggesting that chlorophyll synthesis was impaired. These plants grew more slowly and produced less biomass than did WT. A third group of *dxr*-transformants (four plants designated TIIB) also lacked normal pigmentation in a mosaic pattern.

To determine whether the phenotypic variation observed in the *dxr*-transformants correlated with the expression pattern of the *dxr* transgene, total leaf RNA was isolated for Northern blot analysis by using the DXR cDNA as probe. The results showed that DXR mRNA was strongly expressed in young leaves of WT plants and TI plants (WT appearance) and was easily detected in mosaic plants but not in leaves in which *dxr* was apparently cosuppressed (Fig. 3A). In fully expanded leaves, the DXR message was not detectable in WT (or cosuppressed) plants; however, the level of this transcript increased significantly in proportion to total RNA in TI transgenics and was also observed in TIIB mosaic plants (Fig. 3B). Because the DXP pathway operates in plastids to supply precursor for the biosynthesis of essential metabolites, such as chlorophyll (4, 6), the high-level expression of *dxr* in young leaves is not surprising. As leaves mature, however, the expression levels of many genes, including *dxr*, might be expected to decrease. In transgenic plants, the DXR cDNA was constitutively expressed under control of the CaMV 35S promoter (53). Thus, as leaves mature and many genes are developmentally silenced, the CaMV 35S promoter remains active, resulting in an increase in the proportion of transgene DXR mRNA to total leaf RNA and, as a consequence, may maintain DXP pathway function. In the TIIA group, DXR message was not detectably expressed in immature or fully expanded leaves, as determined by Northern blot analysis (Fig. 3), indicating that the *dxr* gene was cosuppressed (54–56) in these plants. Such down-regulation of *dxr* would very likely compromise chlorophyll biosynthesis and result in the phenotypic lack of pigmentation observed.

To assess DXR activity in transgenic plants, DXR assays were performed with soluble protein extracts from developing leaves of plants in each phenotypic category. These results correlated



**Fig. 3.** Measured mRNA levels for DXR in immature (A) and fully expanded (B) leaves of WT and transgenic peppermint plants. Total leaf RNA was isolated, separated on a denaturing agarose gel (10  $\mu$ g/lane), blotted, hybridized to the radiolabeled DXR cDNA as probe, and exposed to film (Lower). The indicated lanes correspond to: Lane 1, WT plant; Lane 2, transgenic cosuppressed plant; Lane 3, transgenic mosaic plant; and Lane 4, transgenic plant with WT appearance that overexpresses *dxr*. Upper illustrates ribosomal bands visualized with ethidium bromide that were used to verify loading of equal amounts of total RNA before transfer.

well with the Northern blot data, in that extracts of TI plants that over-expressed the DXR cDNA contained two to four times more DXR activity (on a  $\text{nmol}\cdot\text{h}^{-1}\cdot\text{mg}$  of protein $^{-1}$  basis) than did the corresponding extracts from WT plants. Conversely, DXR activity was not detected in extracts of plants in which *dxr* was seemingly cosuppressed, although at least low levels of DXR activity must have been present in these plants because they did grow, albeit slowly, and they were not albino.

**Effects on Essential Oil Production and Composition.** Because glandular trichome metabolism in mint is largely dedicated to monoterpene production driven by precursor supply from the plastidial DXP pathway (7, 12, 34), it was reasoned that alterations in pathway flux because of changes in *dxr* expression should be observable at the level of essential oil accumulation. Essential oil analysis of mint is easily accomplished by steam distillation of leaf tissue followed by gas chromatographic separation of components of the distillate and quantification by using an internal standard (43). These analytical results (Table 1) demonstrated that most plants in the TI group accumulated more oil than WT plants (up to nearly 50% increase in oil yield), whereas plants apparently cosuppressed for *dxr* (TIIA group) produced less oil than did control plants. These analyses further demonstrated that the composition of the essential oil of the transgenic plants was similar to WT in the majority of cases (55 plants). However, two plants produced a significantly different oil composition compared with WT and to the other transgenic plants. One plant (designated DXR16 of the TI group) accumulated higher quantities of menthofuran and pulegone (Fig. 2), whereas a second plant (DXR46 of the TI group) accumulated less pulegone and menthofuran, but more menthol, than did WT plants (Table 1). Additionally, plant DXR46 produced piperitone oxide to a level of about 5% of total oil; this compound was not detected in WT or other transgenic plants. The abnormal oil compositions of DXR16 and DXR46 plants are not consistent with those of other transgenic plants in their respective groups. Thus, it seems likely that these changes in oil profile are not caused by alterations in *dxr* expression but rather are the result of insertional effects of the transgene that

**Table 1. Essential oil yield and composition of WT peppermint and selected transformants expressing the sense version of DXR reductoisomerase (DXR plants) and the antisense version of menthofuran synthase (MFS plants)**

Plant	Oil yield (mg/g fresh weight)	Percentage					
		Limonene	Cineole	Menthone*	Menthofuran	Pulegone	Menthol
WT <sup>†</sup>	1.8	2.4	3.8	45.9	16.8	8.0	6.9
DXR6	2.6	2.0	3.4	45.0	15.7	6.1	12.7
DXR7	2.3	2.0	3.8	55.8	7.2	3.2	11.0
DXR8	2.4	1.9	3.9	45.0	15.5	5.7	12.6
DXR16	1.4	1.8	3.0	23.6	36.4	16.8	6.5
DXR32	2.6	2.2	3.9	46.1	12.5	5.7	13.9
DXR37	2.7	2.2	3.8	47.9	14.7	7.3	13.3
DXR38	2.6	2.0	4.6	50.7	13.7	5.3	13.2
DXR40	2.7	1.7	5.1	62.8	13.6	5.2	13.3
DXR44	2.4	1.9	3.3	38.6	15.0	6.2	11.0
DXR46	1.7	4.8	4.8	45.3	5.1	1.7	27.0
WT <sup>‡</sup>	2.3	1.9	4.6	64.0	5.0	2.0	8.5
MFS1	1.7	1.1	5.3	35.0	2.5	0.2	23.1
MFS3	1.4	1.7	5.8	63.7	2.5	0.7	12.7
MFS7	2.4	1.3	6.3	53.5	2.5	0.8	19.5
MFS15	1.8	1.8	4.0	65.2	3.2	1.3	10.0
WT <sup>§</sup>	1.7	2.3	4.3	60.2	13.9	7.8	4.0
MFS7	1.8	2.6	5.0	68.8	5.3	2.8	7.3

All measurements represent the averages of three replicates of two independent tissue samples, SE  $\pm$  10%. Each group of transformants was compared to WT plants grown under the same conditions.

\*Isomenthone is not included. The combination of menthone plus isomenthone generally constitutes 60–70% of the oil.

<sup>†</sup>This oil composition is typical of newly established plants raised under these moderate stress growth conditions.

<sup>‡</sup>This oil composition is typical of newly established plants raised under these unstressed growth conditions.

<sup>§</sup>This oil composition is typical of established plants raised under these moderate stress growth conditions.

serve, directly or indirectly, to down-regulate pulegone reductase (DXR16) and MFS (DXR46) (see Fig. 2).

In the case of peppermint plants transformed with the antisense version of *mfs*, most (15 plants) produced an oil of near average composition and yield compared with WT (data not shown). However, four of these plants (MFS1, 3, 7, and 15) accumulated 35–55% less (+)-menthofuran (and 40–60% less (+)-pulegone), and substantially more (–)-menthol, than WT controls (Table 1). Oil evaluation over a period of 6 months (four independent distillations and analyses) demonstrated that the MFS7 transgenic plant consistently produced an oil of comparable yield with lower levels of menthofuran and pulegone, and higher levels of menthol, than WT plants. This pattern of uncompromised oil yield and compositional modification persisted even when plants were grown under stress conditions (obtained by elevated night temperature combined with decreased photon flux during the daylight period) that are known to promote the production and accumulation of menthofuran and pulegone (41, 42) (Table 1). It is notable that peppermint plants transformed with *mfs* in antisense orientation (MFS1, 3, 7, and 15) produce an essential oil very similar in composition to the DXR46 plant transformed with the sense version of the reductoisomerase (Table 1), suggesting that the latter bears an insertion that inactivates the *mfs* gene to produce a similar oil compositional change.

## Conclusions

The present results directed to the manipulation of *dxr* as the committed step of the mevalonate-independent pathway to terpenoids support previous findings (24, 57, 58) with *Arabidopsis* in which disruption of *dxps* (the *clal* gene encoding the first step of the mevalonate independent pathway) led to early arrest of chloroplast development and an albino phenotype. In the present instance, both essential oil and chlorophyll biosynthesis were impaired in the *dxr* cosuppressed plants, but it was clear from the visible phenotype and essential oil chemotype that

precursor supply from the DXR pathway was not entirely eliminated in these plants.

Transgenic up-regulation of *dxr*, as evidenced by Northern blot analyses and direct DXR enzyme assays, led to an increase in essential oil accumulation, a result that may be attributed to improved flux of precursors for monoterpene biosynthesis in the oil glands by the increased level or developmental duration of the DXR pathway. Either effect implies that DXR catalyzes a slow step of the mevalonate-independent pathway. It is notable that essential oil yield increases approaching 50% did not result in observable changes in the complex oil composition noted for most plants. This coupling of yield increase without compositional change indicates that the capacity for limonene production (and downstream biosynthetic steps; see Fig. 2) has not been exceeded and thereby suggests that additional rate-determining step(s) reside somewhere between DXR and limonene synthase (the first committed step of monoterpene biosynthesis).

Transgenic down-regulation of *mfs*, by the antisense approach, led to the anticipated decrease in oil content of (+)-menthofuran (without change in yield) but surprisingly did not increase (+)-pulegone content as might be expected via the decreased conversion of this ketone intermediate to (+)-menthofuran (see Fig. 2). Rather, a decrease in the oil content of both menthofuran and pulegone was observed in the transgenic antisense MFS plants (Table 1). This unusual observation is currently unexplained but nevertheless represents a favorable compositional change, because both menthofuran and pulegone are considered undesirable monoterpene components when present in peppermint essential oil at levels exceeding a few percent.

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May 2 2003 16:47:12

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ACCESSION AB009053  
VERSION AB009053.1 GI:2656029  
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ORGANISM Arabidopsis thaliana  
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Magnoliophyta; eudicotyledons; core eudicots; Rosidae; eurosids II;  
Brassicales; Brassicaceae; Arabidopsis.  
REFERENCE 1 (sites)  
AUTHORS Sato,S., Kaneko,T., Kotani,H., Nakamura,Y., Asamizu,E., Miyajima,N.  
and Tabata,S.  
TITLE Structural analysis of Arabidopsis thaliana chromosome 5. IV.  
Sequence features of the regions of 1,456,315 bp covered by  
nineteen physically assigned P1 and TAC clones  
JOURNAL DNA Res. 5 (1), 41-54 (1998)  
MEDLINE 98290546  
REFERENCE 2 (bases 1 to 78145)  
AUTHORS Nakamura,Y.  
TITLE Direct Submission  
JOURNAL Submitted (27-NOV-1997) Yasukazu Nakamura, Kazusa DNA Research  
Institute, Department of Plant Gene Research; 1532-3, Yana,  
Kisarazu, Chiba 292-0812, Japan (E-mail:ynakamu@kazusa.or.jp,  
Tel:81-438-52-3935, Fax:81-438-52-3934)  
COMMENT Address for correspondence: kaos@kazusa.or.jp  
For the latest information on annotation of this clone, please see  
[http://www.kazusa.or.jp/kaos/cgi-bin/agd\\_graph.cgi?c=MQB2](http://www.kazusa.or.jp/kaos/cgi-bin/agd_graph.cgi?c=MQB2)  
Genes with similarity to proteins in the databases are described in  
'product' or 'note' qualifiers. Genes that have no significant  
protein similarity are described as 'unknown protein'.  
The software programs used to predict genes include: Grail  
(Informatics Group, Oak Ridge National Laboratory,  
<http://compbio.ornl.gov/Graill-1.3/>),  
GENSCAN (Chris Burge, MIT, <http://CCR-081.mit.edu/GENSCAN.html>),  
NetGene2 (S.M. Hebsgaard, et al., CBS, Technical University of  
Denmark, <http://www.cbs.dtu.dk/services/NetGene2/>) and  
SplicePredictor (Volker Brendel, Stanford University,  
<http://gremlin1.zool.iastate.edu/cgi-bin/sp.cgi>).  
Genes encoding tRNAs are predicted by tRNAscan-SE  
(Sean Eddy, Washington University School of Medicine, St. Louis,  
<http://genome.wustl.edu/eddy/tRNAscan-SE/>).  
This sequence may not be the entire insert of this clone. It may be  
shorter because we remove overlaps between neighboring submissions.



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The 5' clone is MRG21 and the 3' clone is MJH22.

FEATURES

source Location/Qualifiers

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aug2000

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CDS  
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CDS complement(join(28994..29162,29248..29394,29684..29805,  
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CDS

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78061 tgactcacia
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//

aug2000

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May 2 2003 16:47:12



viewer\_fcgi

LOCUS AB009053 78145 bp DNA linear PLN 27-DEC-2000

DEFINITION Arabidopsis thaliana genomic DNA, chromosome 5, P1 clone:MQB2.

ACCESSION AB009053 BA000015

VERSION AB009053.1 GI:2656029

KEYWORDS .

SOURCE Arabidopsis thaliana (thale cress)

ORGANISM Arabidopsis thaliana  
Eukaryota; Viridiplantae; Streptophyta; Embryophyta; Tracheophyta;  
Spermatophyta; Magnoliophyta; eudicotyledons; core eudicots;  
Rosidae; eurosids II; Brassicales; Brassicaceae; Arabidopsis.

REFERENCE 1 (sites)

AUTHORS Sato,S., Kaneko,T., Kotani,H., Nakamura,Y., Asamizu,E., Miyajima,N.  
and Tabata,S.

TITLE Structural analysis of Arabidopsis thaliana chromosome 5. IV.  
Sequence features of the regions of 1,456,315 bp covered by  
nineteen physically assigned P1 and TAC clones

JOURNAL DNA Res. 5 (1), 41-54 (1998)

MEDLINE 98290546

PUBMED 9628582

REFERENCE 2 (bases 1 to 78145)

AUTHORS Nakamura,Y.

TITLE Direct Submission

JOURNAL Submitted (27-NOV-1997) Yasukazu Nakamura, Kazusa DNA Research  
Institute, Department of Plant Gene Research; 1532-3, Yana,  
Kisarazu, Chiba 292-0812, Japan (E-mail:ynakamu@kazusa.or.jp,  
Tel:81-438-52-3935, Fax:81-438-52-3934)

COMMENT Address for correspondence: kaos@kazusa.or.jp  
For the latest information on annotation of this clone, please see  
[http://www.kazusa.or.jp/kaos/cgi-bin/agd\\_graph.cgi?c=MQB2](http://www.kazusa.or.jp/kaos/cgi-bin/agd_graph.cgi?c=MQB2)  
Genes with similarity to proteins in the databases are described in  
'product' or 'note' qualifiers. Genes that have no significant  
protein similarity are described as 'unknown protein'.  
The software programs used to predict genes include: Grail  
(Informatics Group, Oak Ridge National Laboratory,  
<http://compbio.ornl.gov/Grail-1.3/>),  
GENSCAN (Chris Burge, MIT, <http://CCR-081.mit.edu/GENSCAN.html>),  
NetGene2 (S.M. Hebsgaard, et al., CBS, Technical University of  
Denmark, <http://www.cbs.dtu.dk/services/NetGene2/>) and  
SplicePredictor (Volker Brendel, Stanford University,  
<http://gremlin1.zoology.iastate.edu/cgi-bin/sp.cgi>).  
Genes encoding tRNAs are predicted by tRNAscan-SE  
(Sean Eddy, Washington University School of Medicine, St. Louis,  
<http://genome.wustl.edu/eddy/tRNAscan-SE/>).  
This sequence may not be the entire insert of this clone. It may be  
shorter because we remove overlaps between neighboring submissions.  
The 5' clone is MRG21 and the 3' clone is MJH22.

FEATURES

source Location/Qualifiers

1..78145

/organism="Arabidopsis thaliana"

/mol\_type="genomic DNA"

/strain="Columbia"

/db\_xref="taxon:3702"

/chromosome="5"

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/clone\_lib="Mitsui P1"

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viewer\_fcgi

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CDS complement(join(28994..29162,29248..29394,29684..29805,  
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viewer_fcgi
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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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39661 aatttcttct tctctctttt gttttcccg caatagaaga gacccactt taacatttct
39721 tcgtggagaa ttaaaacccc aaaatgatct agtgtgacgc atgtctatgt gtacctgcac
39781 ctatatgtct ttaaaccaat gatgttgcaa cacgttagtt tataacgcaa tcagatgatt
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40681 agacttgaag gaaaagtcta agaaagtata aaagccacca atactaaaga caccaaaaaa
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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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## viewer\_fcgi

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Boronatdxr

LOCUS AF148852 1775 bp mRNA linear PLN 01-JUN-2000

DEFINITION Arabidopsis thaliana 1-deoxy-D-xylulose 5-phosphate reductoisomerase (DXR) mRNA, complete cds.

ACCESSION AF148852

VERSION AF148852.1 GI:8131927

KEYWORDS .

SOURCE Arabidopsis thaliana (thale cress)

ORGANISM Arabidopsis thaliana  
Eukaryota; Viridiplantae; Streptophyta; Embryophyta; Tracheophyta; Spermatophyta; Magnoliophyta; eudicotyledons; core eudicots; rosids; eurosids II; Brassicales; Brassicaceae; Arabidopsis.

REFERENCE 1 (bases 1 to 1775)

AUTHORS Campos,N., Lois,L.M., Cunillera,N., Carretero,L., Ahumada,I., Hoeffler,J.-F., Pale-Grosdemange,C., Rohmer,M., Ferrer,A. and Boronat,A.

TITLE Isolation and characterization of a cDNA from Arabidopsis thaliana encoding 1-deoxy-D-xylulose 5-phosphate reductoisomerase, the first committed enzyme of the non-mevalonate pathway for isoprenoid biosynthesis

JOURNAL Unpublished

REFERENCE 2 (bases 1 to 1775)

AUTHORS Campos,N., Lois,L.M., Cunillera,N., Carretero,L., Ahumada,I., Hoeffler,J.-F., Pale-Grosdemange,C., Rohmer,M., Ferrer,A. and Boronat,A.

TITLE Direct Submission

JOURNAL Submitted (06-MAY-1999) Bioquímica i Biologia Molecular, Universitat de Barcelona. Facultat de Química., C/ Martí i Franques 1, Barcelona 08028, Spain

FEATURES

source Location/Qualifiers

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# Boronatdxr

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